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Horizontal Intracortical Organization in the Cerebral Control of Limb Movement.*

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It has been widely assumed in theories of brain function that horizontal spread of excitations through the cortex is an important factor in cerebral integration. Not only the irradiation of discrete neural impulses through the fiber feltwork of the cortex, but also the mass conduction of intercellular electrical currents and potentials and the establishment of patterns of "field forces" spreading across the cortex have been presumed to play integrative roles of utmost importance in cerebral organization. The following experiments, however, undertaken to test the influence of such horizontal intracortical organization in the control of limb coordination have failed to demonstrate the existence of any major organizing influence of the sort. Lesions in the cortical arm areas of the monkey (Macaca mulatta) designed to disrupt any patterns of horizontal intracortical conduction either of discrete excitations or of mass electrical currents were found to cause only a slight, almost negligible, interference with motor coordination.

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The lesions consisted of intersecting transverse and longitudinal cuts at intervals of about 2.4 mm made subpially with a thin knife and extending roughly through the depth of the cortex to the underlying medulla. Because the cuts filled immediately with blood, the effect of the operation was to partition the cortex by numerous vertical walls of clotted blood of about 0.08 mm thickness. The cuts interrupted the horizontal transmission of excitations through the cortex itself, but left intact the axon interconnections looping downward through the white matter. These incisions were placed throughout the exposed surface of the cortical arm region including areas 6, 4s, 4, 1, 2, 5, and 7 as represented on architectonic charts with some overlap into the neighboring trunk, leg, and face areas. As a control of the effects of these incisions the corresponding cortical area was destroyed completely by excision in other animals.

The control animals showed a severe paralysis of the contralateral arm and hand which persisted with only slow improvement for a month or longer. In contrast partitioning the area with vertical incisions as described above caused practically no disruption of arm coordination. On the first day after operation no difference was noted in the use of the affected and normal arms in rapid running and climbing movements in a large cage. Even in fine movements of the fingers and hands in manipulating pieces of food, the difference between the normal and affected limbs was very slight. A little weakness in the manipulative finger movements of the affected hand and some preference in such movements for use of the normal hand were the only symptoms noted on the first day after operation. By the seventh day no trace of any motor deficit could be detected. Nor were any sensory or autonomic effects apparent although no special effort was made to test for these. Uninstructed observers could not, even with close study, determine at this time which was the affected arm. Thus although the electrostimulable points in the cortex for movement of shoulder, elbow, wrist, and digits had been separated from each other by incisions as described above, there was no incoordination in the arm and hand movements. The same results were obtained in three unilateral cases. The effects were similar also when lesions of the same type were placed in the opposite hemispheres of these three animals about three weeks after the first operations. Histological examination of the cortex showed that the knife cuts had clearly effected a vertical partitioning of the grey matter as intended.

The surprising lack of disturbance in motor coordination caused by putting multiple vertical partitions in the cortical arm field casts evident doubt on hypotheses of cerebral function which have assumed that horizontal intracortical interaction between and within cortical areas is extensive and an essential element of cortical integration. The experiments indicate that functional interaction between cortical loci is achieved almost entirely by the systems of axons passing through the white matter and that the intracortical interaction *per se* is largely vertical. This is in accord with the descriptions of intracortical synaptic relations presented by Lorente de Nó[1] in which he has pointed out that intracortical connections are established chiefly in the vertical direction with the cells of the various horizontal layers linked together in vertical chains.

Further work is under way to determine the effects of making the incisions increasingly numerous and closer together and also at increased depths into the white matter. Extension of the experiments to the visual cortex has been started.

[1] Lorente de Nó, Chap. XV in *Physiology of the Nervous System* by J. F. Fulton, Oxford University Press, N.Y., Inc., 1943.